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Hybridization in Nature Between Parthenogenetic and Bisexual Species of Whiptail Lizards (Genus *Cnemidophorus*)[1]

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INTRODUCTION

The identity of the type of *Cnemidophorus perplexus* has been uncertain since it was described in 1852 by Baird and Girard. It is one of the senior names in the genus, and consequently there has been ample time during the ensuing confusion for it to be associated with many of the species of *Cnemidophorus* in the United States and Mexico.

The primary aspects of the confusion were two. First, the type locality of the lectotype (U.S.N.M. No. 3060) remained undetermined, and, second, the name represented no known living population.

Maslin, Beidleman, and Lowe (1958) resolved the probable geographic position of the type locality as south of Santa Fe, New Mexico, and subsequently Wright and Degenhardt (1962) verified this conclusion. The critical historical analysis by R. G. Beidleman and the field work of J. W.

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Wright and W. G. Degenhardt, who found Gambel's "Valley of the Rio San Pedro of the Rio Grande del Norte" south of Santa Fe, proved decisive.

In the present report we are concerned with the problem of which actual population the type of *C. perplexus* represents. The decision by Maslin, Beidleman, and Lowe (1958) that the type of *C. perplexus* was a unique specimen, which represented the uniform population described by Lowe and Zweifel (1952) as *C. neomexicanus*, was the best that could be made at that time, if one felt compelled to assign the type specimen of *C. perplexus* to a known population. A prevailing suspicion nevertheless remained that the aberrant type of *C. perplexus* represented a hybrid rather than a member of the species *C. neomexicanus* or of any other.

In 1962 and 1963 six additional specimens of *C. perplexus* were collected in New Mexico. These differ in the same aberrant ways from *C. neomexicanus* as does the type specimen of *C. perplexus*. Three of the six are males, making a total of four females (the type is a female) and three males now known for *C. perplexus*.

In this report we consider in detail the seven individuals of *C. perplexus* and their sympatric congeners. We conclude from the quantitative analysis presented herein, and from our field observations on the ecology of this situation involving sympatric species, that *C. perplexus* is a hybrid form produced by sympatric hybridization involving the maternal species *C. neomexicanus* (parthenogenetic)[1] and the sympatric paternal species *C. inornatus* (bisexual). At points herein we refer to the seven hybrids (= *C. neomexicanus* × *C. inornatus*) singly or collectively by the old name *C. perplexus* (or *perplexus*) wherever it permits greater simplicity in discussion, as in the following section.

METHODS AND MATERIALS

Details for methods of analysis are given at appropriate points in sections that follow. Quantitative analyses followed an experimental design in which the newly acquired specimens of *perplexus* were compared directly with samples of adults drawn from the populations of the parental species at the same localities of sympatric hybridization from which individuals of *perplexus* were taken. Data reductions for single frequency distributions, summarized in tabular form and graphed, involve 95 per cent confidence intervals.

We made special effort to study in the field, to collect adequate series, and to make appropriate observations, with work eventually concentrated

[1] We use interchangeably the terms "parthenogenetic," "unisexual," "uniparental," and "all-female."

at the newly discovered points of sympatric hybridization. Accordingly 150 of the 164 specimens reported on here (tables 1–5) were collected in New Mexico by us; all are deposited either in the Department of Zoology, University of Arizona, Tucson, or in the Museum of Southwestern Biology, University of New Mexico, Albuquerque.[1]

Abbreviations

For the names of institutions:

A.M.N.H., the American Museum of Natural History
M.S.B., Museum of Southwestern Biology, University of New Mexico
M.V.Z., Museum of Vertebrate Zoology, University of California, Berkeley
U.A.Z., Department of Zoology, University of Arizona, Tucson
U.S.N.M., United States National Museum of the Smithsonian Institution, Washington, D. C.

For various terms used in the text:

COS, circumorbital semicircle scales
FP, femoral pores
HI, hybrid index
ILS, interlabial scales
SAB, scales around midbody
SOR, scales between occiput and rump
SPV, scales between paravertebral light stripes
S–VL, snout-to-vent length
TLS, toe lamellar scales

We have been working in the present case with phenotypically discrete characters. There is no approach open at the moment for factor loading for any of them even if such were desirable. The characters and the data reductions employed are those recently conventional for the analysis of variation within the genus (Lowe and Zweifel, 1952; Zweifel, 1959; Duellman and Wellman, 1960; Duellman and Zweifel, 1962; Wright, 1966). They are for the most part phenotypically non-overlapping characters when sympatric populations are considered.

As is noted below, we emphasize repeatedly that, owing to geographic and clinal variation in both parental species, one would not be dealing pre-

[1] The 14 specimens not collected by us, and hence not seen alive or as fresh specimens, are (1) two *C. neomexicanus,* nine *C. inornatus,* and one hybrid (A. L. Gennaro, M.S.B. No. 11613), all from the La Joya locality in Socorro County, and (2) the two specimens from the Valley of the Rio San Pedro collected by William Gambel (U.S.N.M. Nos. 3060 and 30885).

One specimen of the six newly acquired specimens of *perplexus* is now deposited at the United States National Museum (U.S.N.M. No. 154575, female) and two are at the American Museum of Natural History (A.M.N.H. No. 94165, male, and A.M.N.H. No. 94166, female).

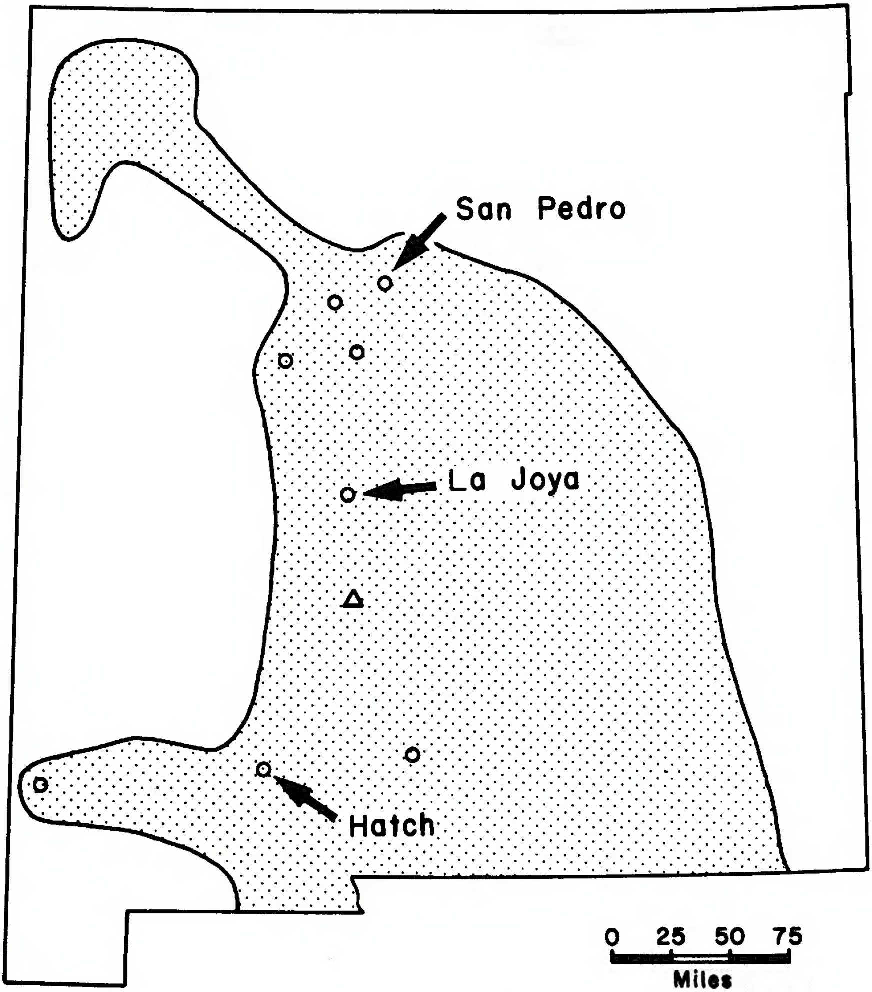

FIG. 1. Arrows indicate the three localities of sympatric hybridization between *Cnemidophorus inornatus* (bisexual) and *C. neomexicanus* (parthenogenetic) in New Mexico. Remaining plots indicate localities of sympatry between the two species, where hybridization is not now known to occur: one of these, indicated by triangle, is the type locality of *C. neomexicanus*. The stippled area indicates the over-all range of *C. inornatus* in New Mexico.

dominantly with non-overlapping and essentially non-overlapping characters if comparisons were made between random samples for variation of each species taken as a whole (over its entire range). There is a distance of more than 200 airline miles between the southernmost and the northernmost of the three localities treated here, and they are situated on an envi-

TABLE 1

SUMMARY OF CHARACTERISTICS OF HYBRIDS AND THEIR PARENTAL SPECIES (95 PER CENT CONFIDENCE INTERVALS) AT THE HATCH LOCALITY OF SYMPATRIC HYBRIDIZATION IN THE GENUS *Cnemidophorus* IN NEW MEXICO

Characteristic	A.M.N.H. No. 94165	U.S.N.M. No. 154575	A.M.N.H. No. 94166	U.A.Z. No. 10577	*C. neomexicanus*	*C. inornatus*
Sex	♂	♀	♀	♀	♀♀	♂, ♀
N	1	1	1	1	24	44
S–VL	57	78	75	79	71.6[a] (70–73)	59.0[b] (57–62)
SAB	65	65	66	65	74.5±0.78 (71–77)	61.4±1.23 (53–70)
SPV	7	7	7	8	10.2±0.90 (9–11)	8.4±0.46 (6–12)
SPV/SAB × 100 (%)	10.8	10.8	10.6	12.3	13.8 (12.2–15.3)	13.6 (9.4–18.8)
COS	8	16	17	16	19.6±0.70 (17–23)	10.2±0.57 (7–16)
ILS	21	28	25	27	27.0±1.01 (21–31)	19.6±0.98 (12–29)
FP	36	37	38	39	38.6±0.61 (36–41)	31.4±0.70 (27–37)
TLS	31	31	31	31	30.7±0.36 (30–33)	26.8±0.53 (24–30)
Stripes	2.5	2.0	2.0	2.0	3.0	1.0
Spots (number)	29	23	22	24	33.8±1.16 (28–38)	0
Spots (definition)	(−)	(−)	(−)	(−)	(+)	—
Leg color	2.0	2.0	2.0	2.0	3.0	1.0
Ventral color	1.0	1.0	1.0	1.0	3.0	1.0
Tail color	1.5	1.5	1.5	1.5	3.0	1.0

[a] Mean and range of five longest specimens in sample (all females).
[b] Mean and range of five longest males in sample.

ronmental gradient through central New Mexico (fig. 1). Any analysis of variation involving comparisons such as those in the present study must take these facts and the associated clinal variation importantly into account, and we have structured our analysis accordingly. The clinal variation in the populations under consideration is similar to that earlier established (Wright, 1966) for the biparental *C. inornatus* as well as for another parthenogenetic species, *C. velox*.

We have observed a total of about 20 presumed genetic features of the parental species; these include characteristics of ecology, behavior, physiology, and morphology. All are useful in the evaluating of the posi-

tions of hybrids. Data reduction for morphological characters, facilitated by electric desk calculator, involved for the original raw data alone somewhat more than 1500 determinations for the 164 specimens. Most of these are summarized in tables 1–3.

SYMPATRIC HYBRIDIZATION

The two parental species occur in sympatry over a broad geographic area, from about Santa Fe, New Mexico, to the vicinity of El Paso, Texas (more or less within the Rio Grande valley), and in some local edaphic situations both east and west of the Rio Grande drainage (fig. 1, map). The two are, in fact, in sympatry at the type localities of both *C. neomexicanus* and *C. perplexus.* Almost the entire geographic range of the uniparental species *C. neomexicanus* is included within that of the wider ranging biparental species *C. inornatus.* Three of the numerous localities of sympatry that we have investigated have yielded *C. perplexus* (i.e., hybrids); these are shown in figure 1 (arrows).

BODY SIZE

Body (snout–vent) length, as an indicator of total body size, is an important character which we have examined in detail that is not of scalation nor of color pattern (see Scalation and Color Pattern). In this section we present the data for body length (with brief comments on other characters) under the discussion of each of the three localities. We refer to these three key localities, and the samples from them, as Hatch, La Joya, and San Pedro.

Hatch: Dona Ana County, New Mexico, at 8.4 Miles West of Hatch (ca. 4600 Feet)

This is the southernmost of the three localities of sympatric hybridization (fig. 1). The habitat is in Plains Grassland and is a localized hybrid habitat modified primarily by some mesquite invasion and sand accumulation.

Four specimens of *C. perplexus,* three females and one male, were among 24 specimens of *C. neomexicanus* and 44 of *C. inornatus* taken together at the same time throughout a small area (*ca.* 30 by 50 yards). This is the only locality of the three under consideration at which we have collected other species of *Cnemidophorus* (*C. tesselatus* and *C. tigris*).

The three female specimens of *C. perplexus* measure 75, 78, and 79 mm. snout to vent, whereas the five largest specimens of *C. neomexicanus* (females) range from 70 to 73 mm. (mean 71.6). The five largest males of the sympatric *C. inornatus* range from 57 to 62 mm. (mean 59.0). The

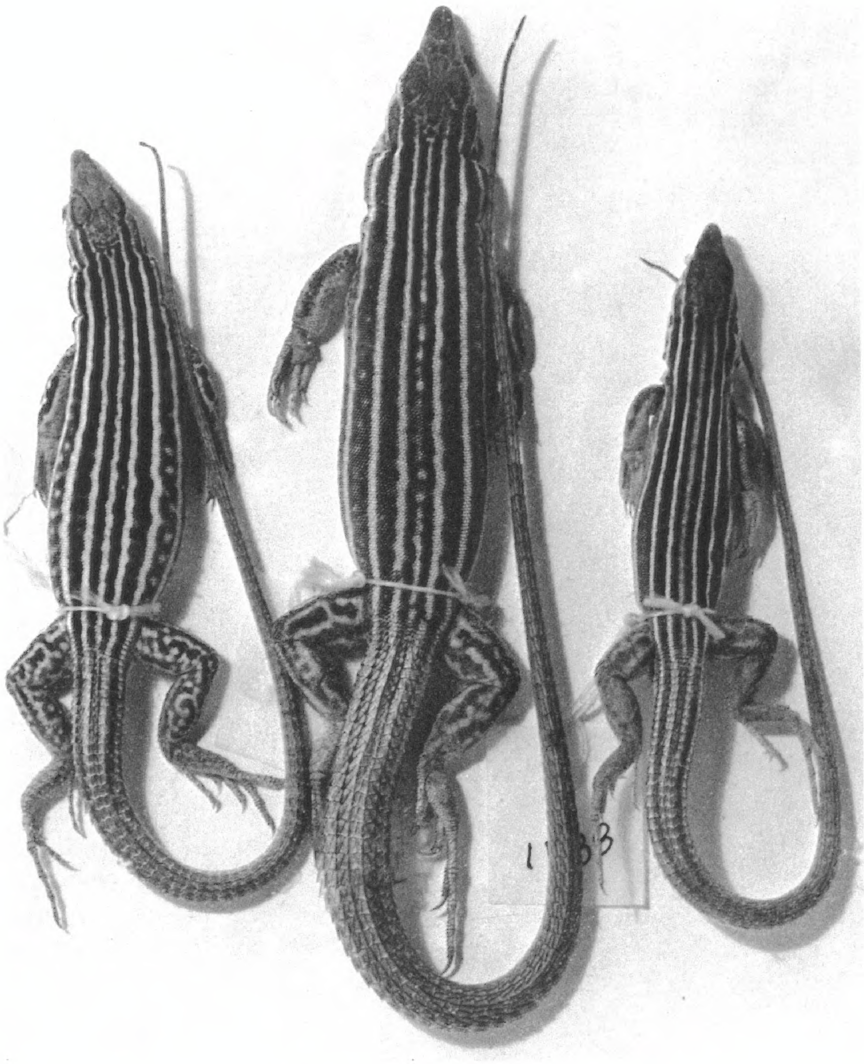

FIG. 2 *Left:* Adult female of *Cnemidophorus neomexicanus* (snout–vent length, 63 mm.). *Right:* Adult male of *C. inornatus* (snout–vent length, 57 mm.). *Center:* Hybrid female (snout–vent length, 78 mm., U.S.N.M. No. 154575). Adult females of *C. neomexicanus* of at least this size or smaller, or both, are inseminated by males of *C. inornatus;* the maximum snout–vent length of female *C. inornatus* at the Hatch locality is 63 mm.

conspicuous largeness of the female hybrids, as indicated by the data for snout–vent length, is of course even more apparent in the body volume

TABLE 2

Summary of Characteristics of Hybrids and Their Parental Species (95 Per Cent Confidence Intervals) at the La Joya Locality of Sympatric Hybridization in the Genus *Cnemidophorus* in New Mexico

Characteristic	M.S.B. No. 11613	U.A.Z. No. 10579	*C. neomexicanus*	*C. inornatus*
Sex	♂	♂	♀♀	♂, ♀
N	1	1	8	25
S-VL	64	69	70.4[a] (68–76)	56.8[b] (55–58)
SAB	69	65	75.8±1.07 (74–78)	62.5±1.74 (52–70)
SPV	9	8	12.5±0.63 (12–14)	7.3±0.56 (4–10)
SPV/SAB × 100 (%)	13.0	12.3	16.5 (15.4–18.4)	11.7 (5.9–14.5)
COS	13	10	16.9±0.83 (16–19)	9.0±0.59 (7–12)
ILS	22	22	20.8±2.08 (17–24)	16.6±1.01 (11–22)
FP	38	38	37.1±0.83 (36–39)	32.1±0.76 (29–35)
TLS	31	31	30.6±0.44 (30–31)	27.3±0.86 (24–31)
Stripes	2.5	2.5	3.0	1.0
Spots (number)	31	26	33.9±3.13 (30–38)	0
Spots (definition)	(−)	(−)	(+)	—
Leg color	2.5	3.0	3.0	1.0
Ventral color	1.0	1.0	3.0	1.0
Tail color	1.5	2.0	3.0	1.0

[a] Mean and range of five longest specimens in sample (all females).

[b] Mean and range of five longest males in sample.

(fig. 2). Heterosis is not apparent in the hybrid male which is relatively small, with a snout–vent length of 57 mm.

The scutellation of all four specimens of *perplexus* is closer to that of *C. inornatus* than to that of *C. neomexicanus,* and is intermediate between these sympatric parents for scale counts around midbody (see table 1). On the other hand, all four specimens are intermediate in pattern or are closer to *C. neomexicanus* than to the spotless *C. inornatus.* Three of the four have lower spot counts than the lowest count for *C. neomexicanus,* and all four fall well below the mean for *C. neomexicanus* (table 1); thus the four individuals of *perplexus* clearly lie intermediate in spotting.

La Joya: Socorro County, New Mexico, at 9 Miles East of La Joya (ca. 5200 Feet)

The locality is in flat, sparsely vegetated Plains Grassland, with some invasion by short shrubs. Perennial and annual grasses remain the conspicuous vegetation components throughout the area.

Two males of *C. perplexus* were taken (see fig. 3). They were among eight individuals of *C. neomexicanus* and 25 of *C. inornatus* collected in the same small area of a few yards in extent. No other species of *Cnemidophorus* was found there.

The largest individual of *C. neomexicanus* from this locality measures 76 mm. from snout to vent; the next largest is 70 mm. The largest male in the sample of *C. inornatus* is 58 mm. The two adult male hybrids, which measure 64 and 69 mm., are intermediate in size between the two sympatric species.

Again, like Hatch (above), the body-scale counts of the hybrids are more similar to those of *C. inornatus* (table 2), the counts for scales around midbody being 69 and 65 compared to the lowest count of 74 for *C. neomexicanus*. Again the color pattern of the two hybrids is somewhat more similar to that of *C. neomexicanus* than to that of *C. inornatus* and, except for ventral body color, is intermediate between the two (tables 2 and 5).

San Pedro[1]: Sandoval County, New Mexico, "Valley of the Rio San Pedro" (San Pedro Creek and Tanque Arroyo, ca. 5300 Feet)

This is the type locality of *C. perplexus* Baird and Girard.

The habitat lies to the east and west of Highway U. S. 85 between Hagan and the Rio Grande (see Wright and Degenhardt, 1962, fig. 1, map). The highway crosses Tanque Arroyo, which is the name of the lowermost extension of San Pedro Creek before it empties (at flood) to the Rio Grande, west of Highway 85. East and west of the new highway bridge which spans the east-west-oriented Tanque Arroyo, the habitat is now a considerably deteriorated stretch of sandy, shrub-invaded Plains Grassland through which courses the almost treeless and dry bed (except at flood) of Tanque Arroyo.

[1] We have found additional hybrids in loan material from James R. Dixon and Philip A. Medica (New Mexico State University). This material, collected in the vicinity of Mesilla, Dona Ana County, New Mexico, was received in December, 1964, and was thus too late to be included in this statistical analysis (hybrid index). A separate analysis has been made of the Mesilla hybrids and parental material and will be reported elsewhere as a joint contribution from the four investigators.

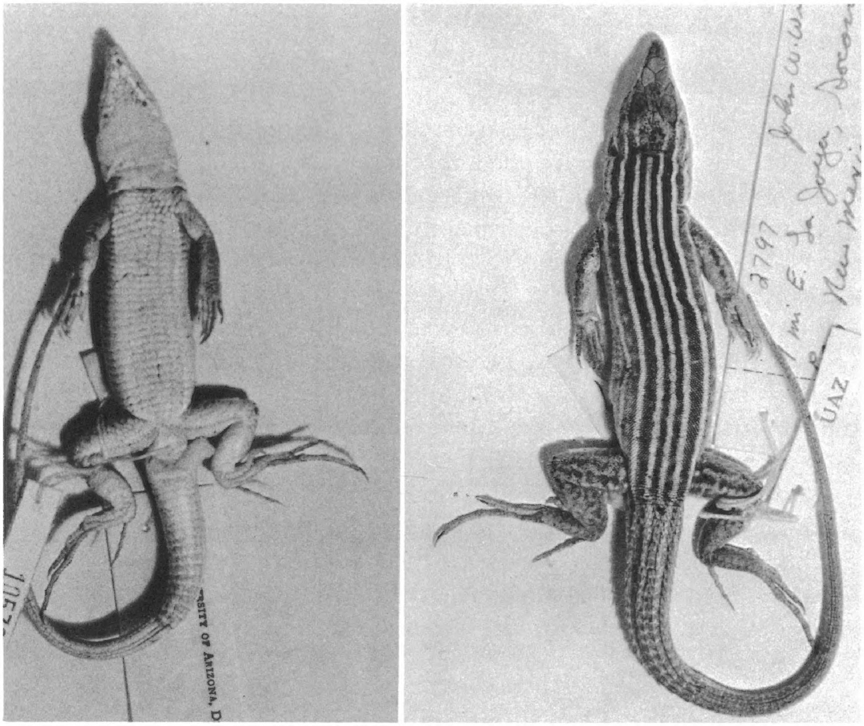

FIG. 3. Male hybrid (snout–vent length, 69 mm.) from 9 miles east of La Joya, Socorro County, New Mexico. *Left:* Ventral view, with hemipenis everted. *Right:* Dorsal view.

The type specimen of *C. perplexus* (U.S.N.M. No. 3060) is compared with samples of 29 specimens of *C. neomexicanus* and 27 of *C. inornatus* from San Pedro Creek[1] and Tanque Arroyo; and an additional sample of three sympatric specimens of *C. inornatus* from Tanque Arroyo. No other species of *Cnemidophorus* is known to occur there.

Body Size and Heterosis

It has been a point of interest to all who have examined the type specimen in recent years (see Discussion below) that it differs conspicuously in its larger body size from all known specimens of the species *C. neomexicanus*. The type is now damaged and stretched, and the original snout–vent

[1] This sample of 27 specimens of *C. inornatus* was collected in the Valley of the Rio San Pedro at San Pedro Creek, at 2 miles east and 3 miles north of San Antonito, Bernalillo County.

TABLE 3

SUMMARY OF CHARACTERISTICS OF HYBRID AND ITS PARENTAL SPECIES (95 PER CENT CONFIDENCE INTERVALS) AT THE SAN PEDRO LOCALITY OF SYMPATRIC HYBRIDIZATION IN THE GENUS *Cnemidophorus* IN NEW MEXICO

Characteristic	U.S.N.M. No. 3060, Type of *C. perplexus*	*C. neomexicanus*	*C. inornatus*
Sex	♀	♀ ♀	♂, ♀
N	1	29	27
S–VL	80[a]	69.6[b] (67–76)	58.9[c] (59–61)
SAB	72	77.8±1.12 (72–83)	65.3±1.46 (58–72)
SPV	12	12.1±0.02 (11–13)	9.3±0.42 (6–11)
SPV/SAV × 100 (%)	16.7	15.5 (14.3–17.1)	14.2 (10.0–16.9)
COS	13	20.3±1.01 (14–25)	8.6±0.33 (8–10)
ILS	25	26.7±1.06 (21–31)	17.6±1.71 (8–24)
FP	38	37.8±1.65 (34–42)	32.1±1.01 (28–36)
TLS	32	32.2±0.40 (31–34)	29.5±0.69 (26–33)
Stripes	2.0	3.0	1.0
Spots (number)	24	32.6±1.10 (28–37)	0
Spots (definition)	(−)	(+)	—
Leg color	2.0	3.0	1.0
Ventral color	1.0	3.0	1.0
Tail color	2.0	3.0	1.0

[a] By regression; see text (fig. 4).
[b] Mean and range of five longest specimens in sample (all females).
[c] Mean and range of five longest males in sample.

length, at the time it was collected 125 years ago, has been a point of recent conjecture. It is now in such a lax condition that a reasonably accurate snout–vent length obtained by direct measurement is no longer possible.

To obtain an accurate estimate of the original snout–vent length of the type, which today can vary from roughly 82 to 91 mm., a regression equation for snout–vent length on snout length (tip of snout to anterior edge of frontal) was calculated (fig. 4) using the six additional specimens of *C. perplexus*. The head of the type, unlike the body, has not obviously

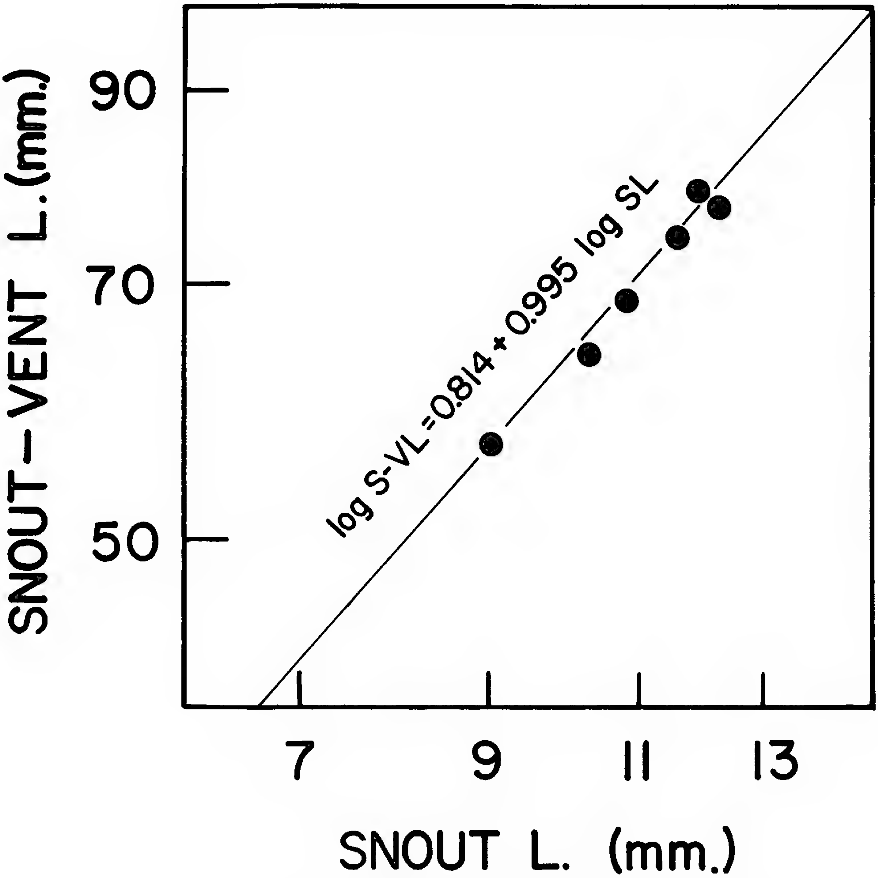

FIG. 4. Regression equation for X on Y (b_{xy}) used to estimate the original snout–vent length (80.4 mm.) of the now-damaged and lax type of *Cnemidophorus perplexus* Baird and Girard (U.S.N.M. No. 3060). Plots represent values for the six additional hybrids collected in 1962–1963; line fitted by least squares.

stretched. Thus the snout–vent length as estimated by regression (log SVL = log a + b log SL) and rounded to the nearest 1.0 mm., is 80 (80.4). The snout–vent length of the largest specimen of *C neomexicanus* from the sample (N = 29) representing the topotypic population is 76 mm., with 69.4 mm. the mean of the five largest. The snout–vent length of 76 mm. for *C. neomexicanus* was the maximum for the species also originally given by Lowe and Zweifel (1952), and 76 is the maximum length for the species as observed in the present investigation involving detailed study of 61 additional specimens.

FIG. 5. *Left:* Type (U.S.N.M. No. 3060, female) of *Cnemidophorus perplexus* (snout–vent length, 80.4 mm.). *Right:* Hybrid female (*C. neomexicanus* × *C. inornatus*) from 8.4 miles west of Hatch, Dona Ana County, New Mexico (snout–vent length, 79 mm.).

Thus, at 80 mm., the female type of *C. perplexus* remains an aberrantly large individual just as do the large females among the newly collected individuals of *perplexus,* one of which is 79 mm. as reported above (Hatch; see fig. 5).

In the sections that follow we repeat the importance of comparing species and their hybrids with material from sympatric or roughly sym-

patric situations. Hence in this study there is a comparison of the type of *C. perplexus* with *C. neomexicanus* from the type locality in northern New Mexico (tables 1–3), rather than a comparison of it with *C. neomexicanus* from southern New Mexico (*sensu* Maslin, Beidleman, and Lowe). This is obviously important, for, as noted, geographic variation and clinal variation occur over the intervening environment gradient of approximately 200 miles.

Thus when characters of the type of *perplexus* are compared with those represented by samples of *C. neomexicanus* and *C. inornatus* from the type locality, the type specimen (U.S.N.M. No. 3060) of *C. perplexus* is found to lie in various intermediate positions between either the ranges or the averages of *C. neomexicanus* and *C. inornatus,* except for body size. At the type locality (San Pedro), as elsewhere in New Mexico, the hybrid that is *perplexus* exceeds in body size that of both of its sympatric parental populations. Heterosis, which is at once observable in the body length, is, of course, even more conspicuous in the body volume and weight in all of the hybrid females known.

In this case, involving interspecific heterosis, the two longest (snout to vent) individuals known (U.A.Z. No. 10577, 79 mm.; U.S.N.M. No. 3060, 80 mm.) exhibit hybrid vigor in the ratios 104 to 100 and 105 to 100, respectively, when the hybrid values are compared with the maximum value known (76 mm.) for snout-to-vent measurement of the largest parental species involved (*C. neomexicanus,* table 3). When the individual means (of five largest from each sample) of the specific parental populations of *C. neomexicanus* are used, the values for hybrid vigor, again beyond this better parent in body size as measured linearly, become 110 and 115 per cent, respectively.

Inasmuch as we have found both parental species to be diploid ($2n = 46$), the heterosis described may be attributed to the allotriploid nature of the hybrid ($3n = 69$, chromosome complements of bone-marrow leucoblasts), having received a diploid complement of 46 chromosomes from parthenogenetic *C. neomexicanus* and a haploid complement of 23 chromosomes from the male parent (*C. inornatus*). A detailed karyotypic analysis is in progress.

SCALATION AND COLOR PATTERN

Body size of the seven hybrids and of their sympatric parental populations is treated in the preceding section. Eleven additional characteristics have been analyzed in similar detail—six of scalation (plus a ratio, SPV/SAB), three of color pattern, and two of color (tables 1–3). Hybrid indices for each of the seven individuals are given in table 4.

In addition we have concerned ourselves with several other pertinent quantitative and qualitative aspects of the variation of these species; hybrid indices have not been determined for such features. As in the experience of most taxonomists, many such features are subtle and are of utility for the investigator who has a well-developed "feeling" for the species in question. But seldom are these characteristics readily quantified or otherwise easily well analyzed. For example, we call attention to the definition (or diffuseness) of the light spots in the dorsal dark fields (tables 1–3; figs. 2, 3, 5), one of such very real but subtle differences which obtain between *C. neomexicanus* and the hybrid, *C. perplexus; C. inornatus* is unspotted.

Hybrid Index

It was found fully satisfactory for present purposes to use a simple hybrid index that has been successfully employed in other vertebrate groups (Hubbs and Kuronuma, 1942; Sands and Findley, 1959). It is also apparent that a still more simplified index (e.g., Anderson, 1949, and elsewhere) would have sufficed quite well to answer our particular question in regard to *C. perplexus* (viz., hybrid origin), but without the additional desired sensitivity.

For calculations of the hybrid index (HI, hybrid position in per cent) on the distance from 0 to 100, the sample mean for each distribution of *C. inornatus* was set on the scale at 0 and the corresponding means for *C. neomexicanus* at 100. Thus $\bar{x}_1$ is the mean for *C. inornatus* and $\bar{x}_2$ is the mean for *C. neomexicanus* in the equation

$$\mathrm{HI} = \frac{X_h - \bar{x}_1}{\bar{x}_2 - \bar{x}_1} \times 100,$$

in which X_h is the value of a given character of a presumed hybrid; $\overline{X}_h$ is the mean of a sample (Hubbs, Hubbs, and Johnson, 1943).

Scales Around Midbody

The Count: The prevailing lack of a standard reference point that is precise for initiation of the count, even within the work of a single investigator, remains an undesirable situation. The question is simple—Where is midbody?—as can be the answer.

The standard reference point for the initiation of the count for scales around midbody, in our work in the present investigation and others, is the tip of the ventral scute in the outermost row which is adjacent (lateral) to the fifteenth scale of the second row. The fifteenth scale (or any other) is determined by counting posteriorly from the area of the axilla

TABLE 4

HYBRID INDICES (IN PER CENT) FOR SEVEN HYBRIDS (*Cnemidophorus neomexicanus* × *C. inornatus*) BASED ON SAMPLE STATISTICS OF THE PARENTAL SPECIES FROM THREE SYMPATRIC POPULATIONS

	Hatch				La Joya		San Pedro
	A.M.N.H. No. 94165, Male	A.M.N.H. No. 94166, Female	U.S.N.M. No. 154575, Female	U.A.Z. No. 10577, Female	M.S.B. No. 11613, Male	U.A.Z. No. 10579, Male	U.S.N.M. No. 3060, Female
SAB	28	35	28	28	49	19	55
SPV	<0	<0	<0	<0	33	14	96
COS	72	62	<0	62	51	51	38
ILS	>100	73	19	>100	>100	>100	81
TLS	>100	>100	>100	>100	>100	>100	93
FP	78	92	64	>100	>100	>100	>100
Stripes	75	50	50	50	75	75	50
Spots	68	65	86	71	91	77	74
Hind leg	50	50	50	50	75	100	50
Tail	50	25	50	25	25	50	50

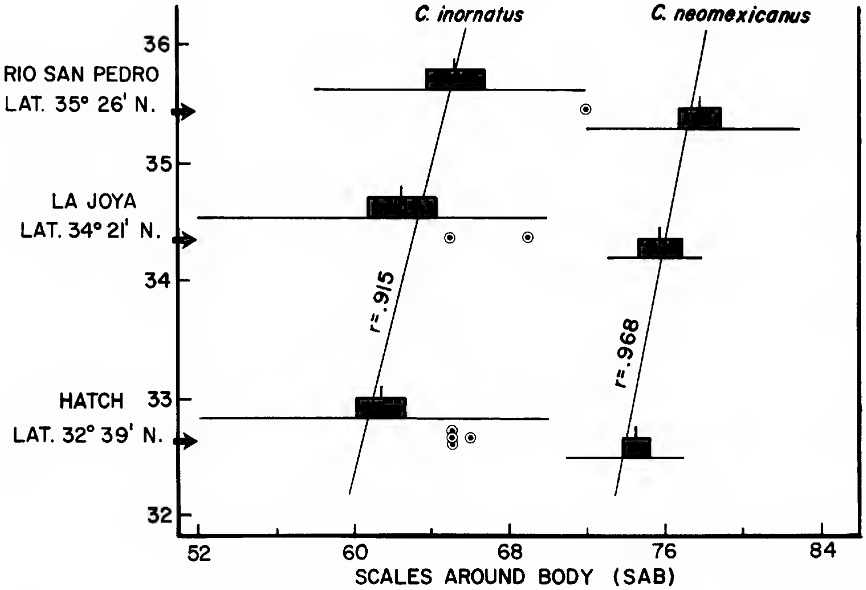

FIG. 6. Clinal variation in scales around midbody for the parental species (*Cnemidophorus inornatus* and *C. neomexicanus*) in New Mexico. The seven hybrids are indicated by dotted circles. Data in tables 1–3; hybrid indices in table 4.

(origin of ventral rows) in the second row of ventrals; the second row parallels the lateralmost (outermost) ventral row at midbody. This lateralmost row, which contains the standard reference scale in question, ordinarily does not extend anteriorly (as a row of enlarged ventrals) as far as the axilla; hence the necessity of counting in the second row to find the fifteenth scale.

THE PARENTAL SPECIES: Both parental species, *C. inornatus* and *C. neomexicanus*, show a clinal increase in SAB from south to north (fig. 6). The extent of this cline in both species is such that the sample means from Hatch (southernmost) are significantly different ($P < 0.01$) from the corresponding means from San Pedro (northernmost), whereas the means obtained from the geographically intermediate La Joya are intermediate values, as expected.

THE HYBRIDS: Hybrid indices for six of the seven hybrids are under 50 per cent, and the index exceeds 35 per cent in only two of the specimens (table 4). As shown in tables 1–3, all seven of the hybrids fall within the range of scales around midbody of *C. inornatus*, and one of these barely reaches the lower extreme for *C. neomexicanus*. This individual is the type of *C. perplexus* (U.S.N.M. No. 3060) which has scales around midbody

of 72; this count, 72, is the upper extreme for *C. inornatus* and the *lower* extreme for *C. neomexicanus* at San Pedro (tables 1–3; fig. 6).

Scales Between the Paravertebral Light Stripes

The Count: The number of scales that fall between the paravertebral light stripes at midbody is taken as the count. Hence a value for scales between the paravertebral light stripes involves both a character of scalation and one of color pattern (dorsal light striping). Accordingly, it reflects, in part, the variation in the amount of middorsal separation of the paravertebral light stripes as well as stripe width, both of which may be irregular at midbody. Thus, although the count of the scales between the paravertebral light stripes is ordinarily made along the transverse row used for the count of scales around midbody, it may be desirable, because of stripe irregularity in some cases, to average the situation for a few rows both anteriorly and posteriorly to the midbody row, in order to obtain a more representative count of the scales between the paravertebral light stripes for a given specimen.

The percentage which indicates the quantity of scales between the paravertebral light stripes involved in the scales around midbody is given by SPV/SAB $\times$ 100. The values for this ratio are given in tables 1–3. In the present study we have used the means of the primary data for scales between the paravertebral light stripes (and scales around midbody) in the determination of hybrid indices (tables 4 and 5).

The Parental Species: For all three of the localities involved, the number of scales between the paravertebral light stripes for the two parental species is significantly different ($P < 0.01$), with *C. inornatus* lower. Clear-cut clines in numbers of scales between the paravertebral light stripes in New Mexico are not observed within either species, although a trend that is similar in both species is apparent. Thus, in *C. neomexicanus* the southernmost locality (Hatch) has significantly lower values for scales between the paravertebral light stripes than those for La Joya (central) and San Pedro (northernmost), and in *C. inornatus* the sample from La Joya has lower values than the sample from San Pedro.

The Hybrids: The four hybrids from Hatch have counts for scales between the paravertebral light stripes that are well within the range of *C. inornatus* and below the range of *C. neomexicanus,* even though the ranges in the counts for the scales between the paravertebral light stripes for the two sympatric populations overlap. The values for the hybrids from La Joya and from San Pedro all fall between the means for the parental species drawn from their respective localities.

A trend in the numbers of scales between the paravertebral light

stripes is apparent (table 4), the value for individual hybrid indices being negative (< 0) in the south (Hatch), 14 and 33 at La Joya, and 96 in the north (San Pedro). Although the total sample involved is small (seven), we note that this apparent trend conforms roughly with that of the parental species (tables 1–3) both of which are also highest at the northernmost station (San Pedro).

For the ratio, the same apparent latitudinal trend emerges as for scales between the paravertebral light stripes (see tables 1–3) and scales around midbody (see fig. 6) when treated singly. The individual ratios for the hybrids lie within the ranges of variation of one or the other of the parental species (tables 1–3).

Scale Rows Between Occiput and Rump

See Lowe and Zweifel (1952), Lowe (1955), and Zweifel (1959) for the advantages, disadvantages, and comparisons of this count with that for the scales around midbody. The count can be made accurately if it is attempted not directly on the vertebral midline, but rather to one side of it, counting rows, beginning with the first granular row posterior to the enlarged scales of the occiput and ending with the last granular scale row before the scale enlargement and keeling on the rump.

In the present study we have used the midbody and paravertebral counts, not the occiput-to-rump count, to represent characteristics of the body scales for hybrid indices.

Circumorbital Semicircle Scales

The Count: The count can be made in different ways, with very different resulting numbers. In the present case it was made by our starting at the anterodorsal edge of the enlarged temporal[1] and counting the single scale row (= circumorbital semicircle) that begins at this position and runs medially and then anteriorly between the frontal and the supraorbitals. Anteriorly the series ends abruptly and ordinarily before the prefrontal scale is reached. The raw-data value used for each individual is the sum of the counts for both sides of the head (fig. 7), a very useful and quickly read character.

Ordinarily at the posterior end of this series, in both species and their hybrids, there is a shorter and conspicuous row of scales that lies anteroventrally to the circumorbital row. They are not included in the count.

The Parental Species: In all cases, the means for the number of cir-

[1] This relatively large scale is occasionally called "supratemporal" or "enlarged supratemporal." It is in essentially the same position in both parental species (see fig. 7).

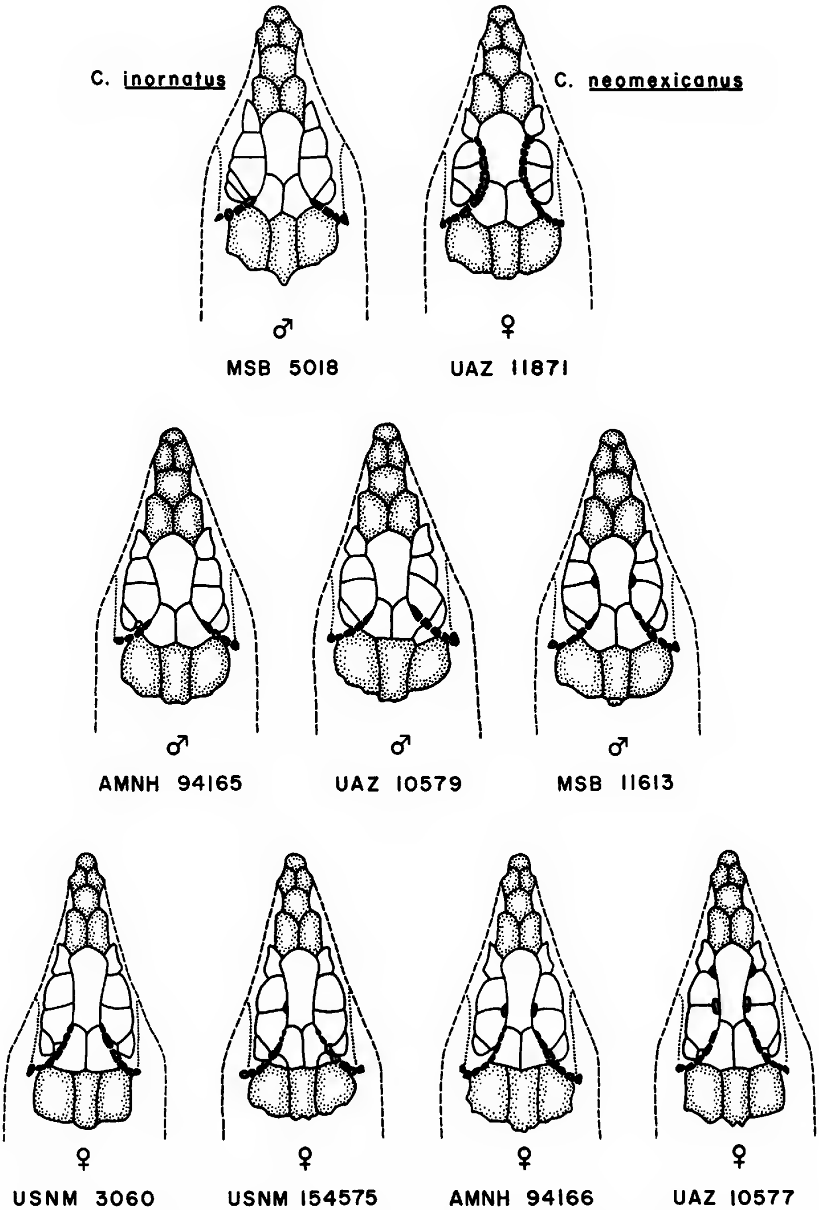

FIG. 7. Dorsal head scales of seven hybrids (*Cnemidophorus neomexicanus* × *C. inornatus*) and individuals representing their parental species, illustrating degree of development of the circumorbital semicircle scales. Enlarged to approximately same scale.

cumorbital scales in *C. inornatus* are significantly lower ($P < 0.01$) than the means for *C. neomexicanus* (tables 1–3). There is a clinal increase in the means in *C. inornatus* from north to south, with significant differences between the southernmost and northernmost samples.

The count for circumorbital scales indicates the number of scales in the semicircle series. It does not directly express the related extent of the separation of the median head plates from the supraoculars. As earlier workers have pointed out, the fourth supraocular and nearly three-fourths of the third (see below) is separated (by the circumorbital scales) in the type of *C. perplexus* (fig. 7), whereas *C. neomexicanus* usually has the fourth, third, and often the second separated; we should add that in *C. neomexicanus* at least part, and very frequently all, of the second supraocular is separated.

THE HYBRIDS: The hybrid indices (table 4) indicate the same clinal trend (increase from north to south) for the hybrids that is seen in the frequency distributions for *C. inornatus* (tables 1–3).

Of the four hybrids from Hatch, three fall essentially between the frequency distributions for the two parental species, and the fourth falls near the mean of *C. inornatus* (tables 1–3). The two male hybrids from La Joya, with values of 10 and 13, again lie between the means of the two parental samples and are both similar to the distribution for *C. inornatus,* and well separate from that of *C. neomexicanus*. At San Pedro, the hybrid type again lies between the ranges of the frequency distributions for the two parental species.

All the hybrids have the fourth supraocular and some part of the third separated (one-third to two-thirds) from the median head plates (fig. 7). Three of the hybrids possess a single disjunct scale that lies at the suture of the second and third supraoculars on each side of the head. In addition, one of the three (U.A.Z. No. 10577) has a single disjunct scale at the suture of the first and second supraoculars on both sides. This same specimen represents the maximum development of the circumorbitals in the hybrids. We estimate the type of *C. perplexus* to be two-thirds of the third supraocular, rather than three-fourths of it as described by Maslin, Beidleman, and Lowe (1958). The general condition in *C. inornatus* has all of the fourth supraocular and one-eighth to one-fourth of the third separated. The hybrids in general lie intermediate between *C. inornatus* and *C. neomexicanus,* but slightly closer to *C. inornatus,* as the counts of the number of circumorbital scales also indicate.

Interlabial Scales

The Count: The interlabials are small scales that separate the chin shields from the infralabials. The arrangement of them is essentially that of a single row of scales of decreasing size anteriorly from near the angle of the mouth. The counts for the two sides of the head were added, and the sum was used as the single observation for analysis. The anteriormost of the series are often very tiny and may be covered (hidden) by infralabials.The count was made with the aid of magnification, and none of the hidden scales were included in the total.

The Parental Species: Here, as elsewhere in the analysis of scale characters, samples of *C. inornatus* have lower means than the corresponding samples of *C. neomexicanus* (tables 1–3). Clines in the numbers of interlabial scales are not indicated for either species, although geographic variation is apparent.

The Hybrids: The situation is one in which all hybrids are closest to the condition in *C. neomexicanus,* yet with individual values that fall just within or just outside the upper range limit for *C. inornatus* (tables 1–3).

The individual hybrid indices appear to be more than usually variable (table 4), primarily because of the condition of a single individual. This one hybrid female from Hatch (A.M.N.H. No. 94166) has consistently lower values for several characters of scalation than do the other three hybrids from the same locality (tables 1–3).

Femoral Pores

The Count: Commonly there are more femoral pores on one thigh than on the other. The number of pores on the under side of each thigh was counted, totaled, and the sum was used as a single value to represent the specimen for analysis.

The Parental Species: There appear to be no clinal trends in the number of femoral pores, or significant geographic variation of any kind. The means for the two species are significantly different and well separated. The ranges of their frequency distributions are distinctive, being either slightly separated or slightly overlapping according to locality.

The Hyrids: All seven hybrids are similar to *C. neomexicanus.* The hybrid values range from 36 to 39 pores, a range that encompasses the means for all of the samples of *C. neomexicanus.* The number of femoral pores of only two of the seven hybrids fall within the range of *C. inornatus* (tables 1–3).

In this feature of the leg, as in the number of toe lamellar scales of the foot (see below), the hybrids resemble more closely the larger of the parental species, the maternal *C. neomexicanus.* This resemblance is re-

flected in the sample hybrid indices (95% and 92%) for these characters of the extremities, which are the two highest mean indices obtained in the present study (table 5).

Toe Lamellar Scales

The Count: This is the number of the ventral toe lamellae on the longest toe (fourth) of one hind foot; the count was made on the left side. These scales are greatly enlarged and are well separated from the more granular scales of the sole of the foot, so that the toe lamellar scales are well defined and relatively easy to count accurately under magnification.

The Parental Species: In all comparisons of sympatric populations, the means for the number of toe lamellar scales for *C. inornatus* are significantly lower than those of *C. neomexicanus* (tables 1–3). In *C. inornatus* there is clinal increase from south to north. Moreover, the northernmost sample mean for *C. neomexicanus* is also significantly higher than those southward.

The Hybrids: The individual hybrid indices are uniformly high (table 4), and the mean index (table 5) for the number of toe lamellar scales of all seven hybrids (92%) is exceeded only by that for femoral pores (95%), as noted above. Six of the seven hybrids have counts of 31, and all seven are closer to the means for *C. neomexicanus,* as is clearly reflected in the high indices for each. At the two northernmost localities the three hybrids available also fall within the statistical range of *C. inornatus* (tables 1–3).

Spots

The Count: The total number of light spots occurring in both (left and right) upper lateral dark fields af *C. neomexicanus* and the hybrids was counted. The sum for each specimen was used in analysis. The accuracy of the count is close to plus or minus one spot. In all cases, the spots of the hybrids are more diffuse (ill defined) than in the case of the parental samples (tables 1–3; figs. 2, 3, 5).

The Hybrids: Spotting is conspicuously reduced in the hybrids (figs. 2, 3). At Hatch, three of the four hybrids have values below the entire range for *C. neomexicanus* from all localities ($N = 59$; fig. 8). At La Joya, one of the two is below the range of local *C. neomexicanus,* and the other is barely within it (tables 1–3).

At San Pedro, the type specimen (U.S.N.M. No. 3060) is again below the range for the San Pedro *C. neomexicanus* and nearly 10 spots below the mean. The type is given a "generous" count of 24 (plus or minus one or two); this is consistent with its somewhat faded color pattern which is, in fact, in remarkably good preservation today and with the 12 or 13

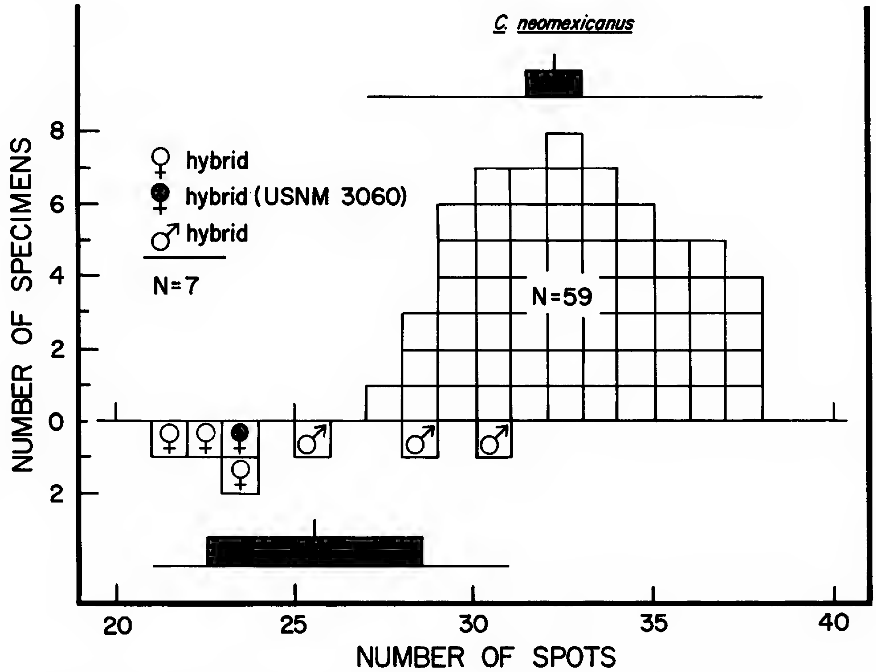

FIG. 8. Frequency distributions for the total number of light spots in both (right and left) upper lateral dark fields of *Cnemidophorus neomexicanus* and seven hybrids; *C. inornatus* is not spotted (reduced data in tables 1–3).

spots in each field as reported by Maslin, Beidleman, and Lowe (1958). It is of interest to note that the mean of the six newly acquired hybrids is 25.8, which compares favorably with the 24 assigned to the preserved type.

The seven individual hybrid indices, which range from 68 per cent to 91 per cent, with a mean of 76.0 (table 4), indicate clearly the closeness in this feature to the maternal species, in spite of the fact that the amount of spotting is conspicuously reduced in the hybrids in both quantity and definition (discreteness).

STRIPES

THE ANALYSIS: Analysis concerns the longitudinal light stripes on the upper surface of the body (figs. 2, 3, 5) and centers on the nature of the middorsal stripe, which is highly characteristic (diagnostic) in *C. neomexicanus* and markedly less so for *C. inornatus* (populations in New Mexico).

We assigned a value of 3.0 to the *neomexicanus* condition at each locality and judged degree of departure toward the condition in *C. inornatus*,

to which we assigned a value of 1.0. A total of five values was thus available for assignment within each group of parental types and their hybrids from the same locality (i.e., 1, 1.5, 2, 2.5, and 3). We treated each locality separately and judged each hybrid on the basis of the parental samples from only that locality. Thus, a hybrid assigned a value of 2.0 by the method employed might receive a value of 2.5 or some other if it were compared with parental samples from another locality.

THE PARENTAL SPECIES: The distinct and wavy (zigzag) middorsal stripe of *C. neomexicanus* is characteristic and also relatively stable. Occasionally the stripe is slightly parted (divided), and traces of dark body color may be apparent between the half lines, but in no case is it parted enough to be considered two stripes. In most cases the stripe is bifurcate at the occiput, with continuous lines forming a Y; in some only a pair of light dots marks the position of the usual bifurcation.

The middorsal stripe of *C. inornatus* is not wavy, and it is far more variable in intensity and presence than its counterpart in *C. neomexicanus*. It can vary from nothing more than a short "tick" at the occiput to distinctive completeness with partial division, and there are many degrees of intermediacy in both extent and distinctness.

THE HYBRIDS: Variation in the stripes of the hybrids is not great, and the range is 2.0 to 2.5 (tables 1–3). The values indicate intermediacy, with somewhat greater closeness to the condition in *C. neomexicanus;* the midstripe is conspicuously less wavy (less zigzag) than in *C. neomexicanus,* and there is general reduction in the distinctness of all the stripes. All hybrids also have a degree of midstripe bifurcation at the occiput, although it is reduced from the pronounced condition in *C. neomexicanus.*

Although the seven individual hybrid indices vary from 50 to 75 per cent (table 4), the mean of 60.7 indicates the consistently wider departure in striping than in spotting (mean, 76.0%) from the condition in the maternal species—the species that the hybrids most closely resemble in general dorsal body pattern.

LEG COLOR PATTERN

THE ANALYSIS: As in the analysis of other features of color pattern, the pattern on the dorsal surface of the thigh in *C. neomexicanus* was assigned the value 3.0, at the high end of the scale involving five assignable values.

THE PARENTAL SPECIES: No clines are apparent (tables 1–3). In *C. neomexicanus* the upper femoral surface is very boldly marked with contrasting light (cream color) areas on the dark ground color (fig. 2). In general, the light areas (or lines) tend to anastomose and to impart the definite im-

pression of a complex reticulum or mottled pattern. Also, two or three widely spaced light linear areas (or lines) run the length of the posterior upper surface of the thigh. As a rule, approximately 50 per cent or more of the total dorsal surface of the thigh is thus occupied by light areas.

In *C. inornatus* generally less than 25 per cent of the femoral surface is light colored. The specimen photographed in figure 2 represents about the maximum condition, which is greater than 25 per cent. In contrast, some specimens are uniformly dark over the entire upper surface. In most individuals there is a light reticulum or mottling of some degree, and there are usually two linear light areas (or lines) present on the dorsal surfaces, similar to the situation in *C. neomexicanus* but of much lesser contrast to the dark ground color (fig. 2).

The Hybrids: The values assigned the hybrids range from two to three, with associated hybrid indices of 50 to 100. As with spotting and striping, regardless of the sex of the hybrid the femoral color pattern is conspicuously more similar to the condition in the maternal species *C. neomexicanus* than to that of the bisexual paternal species *C. inornatus* (tables 1–4).

Ventral Body Color

The Analysis: Comparisons were made by the method similar to that employed for tail color, femoral pattern, and dorsal light stripes (above). The analysis of color (as distinct from color pattern) presents additional problems. All specimens evaluated were collected and preserved by us, except as noted above (Methods and Materials). The exceptions include two hybrids: one male from La Joya and the type specimen from San Pedro (U.S.N.M. No. 3060). Consequently data for colors in life of most hybrids are available. All of La Joya lizards collected by A. L. Gennaro are well preserved and do not differ in any appreciable way from the La Joya specimens collected by us a year later. The two specimens collected by Gambel (one is a male *C. inornatus*) are now 125 years in preservation and are obviously faded. The type, however, is in remarkably good preservation for color-pattern analysis, considering its age, and has quite definitely maintained indications of life colors.

The Parental Species: Marked sexual dimorphism in ventral body color exists between the males and females of *C. inornatus*. This dimorphism is in the amount and intensity of blue pigmentation (relative darkness) rather than the presence or absence of blue color. Samples of the unisexual *C. neomexicanus*, on the other hand, tend to be uniformly immaculate white (pearl), with a slight greenish to greenish blue cast on the corresponding ventral body surfaces.

The Hybrids: Each of the new hybrids is richly pigmented with blue

on the ventral body surfaces, thus rendering them similar to *C. inornatus* in this feature. In fact, each of the female hybrids possesses more blue than normally would be expected to be present in females of *C. inornatus*. The male hybrids possess slightly more blue than do the female hybrids, and are in the general range of male *C. inornatus*. Accordingly, the resulting values assigned for each hybrid were 1.0, as in *C. inornatus* (tables 1–3).

Tail Color

The Analysis: The analysis for hybrid position was conducted in the same manner as that for the previous qualitative features (above).

The Parental Species: The dominant tail color of *C. neomexicanus* is olive-green, but a pale greenish blue occurs in some individuals, especially toward the tip of the tail. Sexual dimorphism exists in *C. inornatus*, with males tending to have deeper and more extensive coloring than females. The dominant tail color of *C. inornatus* is blue; the blues range from light pastels to darks (and almost purple). Greens of any shade are for the most part lacking. The difference in tail color between these two species is, in fact, a sharp difference that is not easily confused once noted.

The olive-green color of *C. neomexicanus* was assigned a value of 3.0, and the blue of *C. inornatus* a value of 1.0. In view of the sexual dimorphism in *C. inornatus* (males darker blue), the sex of the hybrid was considered in the color evaluation.

The Hybrids: For the most part only slight differences between the hybrids and *C. inornatus* were noted, and most were assigned a value of 1.5. There were two exceptions. One of the males from La Joya, collected by us, was assigned a value of 2.0; the corresponding hybrid index (50%) represents the closest approach to *C. neomexicanus* in this character. The other exception, of similar nature, was the type specimen from San Pedro, which now lacks the distal portion of the tail and is in general somewhat faded. We assigned this specimen a value of 2.0, inasmuch as the only distinguishable color remaining appears as a light blue. The original intensity of color cannot now be determined (tables 1–3).

DISCUSSION

Hybrid Indices

Hybrid indices, and the means and confidence intervals for the frequency distributions of the parental species, are given in table 5. The overall mean (mean of means) hybrid index representing all characters analyzed for all hybrids is 50.4 per cent, indicating over-all intermediacy of the seven hybrids in the sample at hand.

Taken as a group, the seven hybrids bear closer resemblance to *C. inor-*

TABLE 5

SUMMARY OF MEANS (WITH 95 PER CENT CONFIDENCE INTERVALS) FOR POOLED SAMPLES OF EACH SPECIES OF *Cnemidophorus* AND A SAMPLE OF SEVEN HYBRIDS FROM NEW MEXICO[a]

Character	*C. inornatus* $N = 91\text{–}96$	All Hybrids $N = 7$	*C. neomexicanus* $N = 59\text{–}61$
COS	9.5 ± 0.35	13.3 (38%)	19.6 ± 0.61
ILS	18.3 ± 0.73	24.3 (78%)	26.0 ± 0.85
SAB	62.8 ± 0.87	66.7 (29%)	76.2 ± 0.72
SPV	8.3 ± 0.30	8.3 (0%)	11.4 ± 0.29
FP	31.7 ± 0.46	37.7 (95%)	38.0 ± 0.81
TLS	27.7 ± 0.42	31.1 (92%)	31.4 ± 0.30
Spots	0.0	25.6 (78%)	32.7 ± 0.72
Dorsal stripes	1.0	2.1 (55%)	3.0
Ventral color	1.0	1.0 (0%)	3.0
Tail color	1.0	1.6 (30%)	3.0
Femoral pattern	1.0	2.2 (60%)	3.0

[a] See tables 1–4. Hybrid indices (to nearest 1.0%) are given in parentheses and are graphed in figure 9.

natus in the following characters: scales around midbody, scales between paravertebral stripes, circumorbital semicircle scales, ventral body color, and tail color (fig. 9). The hybrids are closer to *C. neomexicanus* in number of femoral pores, toe lamellar scales, interlabial scales, spotting, striping, and femoral color pattern (fig. 9). The female hybrids exceed either parent in their maximum body size, which appears to be on the order of 80 mm.; none of the three known males is particularly large (57, 64, and 69 mm. snout to vent), but they show a tendency to be larger than males of *C. inornatus*.

Four specific characters among those we have studied have been considered previously (Lowe and Zweifel, 1952; Maslin, Beidleman, and Lowe, 1958; Duellman and Zweifel, 1962; Wright, 1966) as primary features to be analyzed for the species in question: (1) scales around midbody, (2) circumorbital semicircle scales, (3) spots, and (4) stripes. The over-all mean hybrid index for the first three of these taken as a group is 48.3 per cent. When all four characters are averaged, the index mean is 50.0 per cent.

Thus it is of interest that with the analysis of seven additional characters in the present study, making a total of 11 for hybrid indices (an additional seven that involved more than 1000 measurements and the

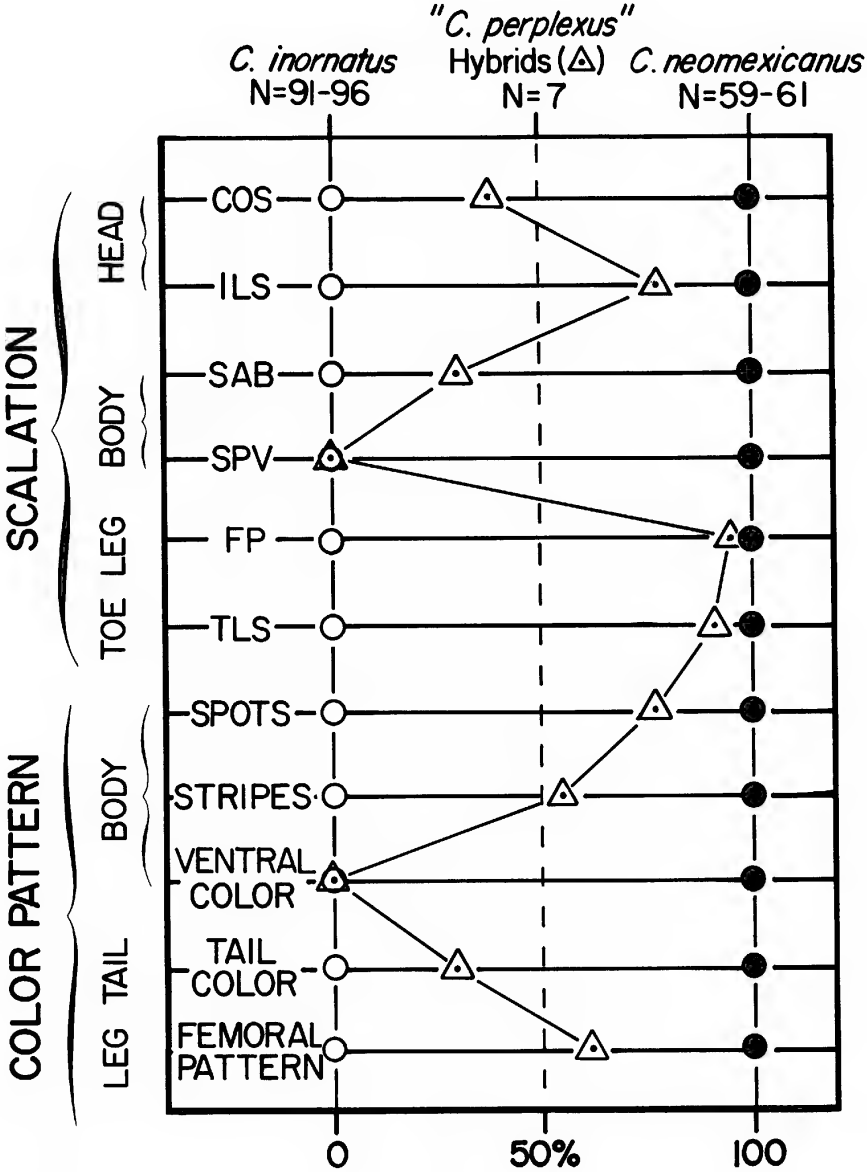

FIG. 9. Graph of hybrid indices for 11 characters of a sample of seven hybrids (triangles) based on pooled-sample statistics for each of the two parental species. Data in table 5.

Abbreviations: COS, circumorbital scales; FP, femoral pores; ILS, interlabial scales; SAB, scales around midbody; SPV, scales between the paravertebral light stripes; TLS, toe lamellar scales.

data reductions for them), the change in the grand mean hybrid index is, accordingly, from 50.0 to 50.4, a difference of less than 1 per cent.

Nomenclature

As noted above, one of the hybrids of the seven now available is the type specimen (lectotype, U.S.N.M. No. 3060) of *C. perplexus* Baird and Girard. Its aberrant peculiarities, which depart conspicuously from the characters of *C. neomexicanus* Lowe and Zweifel, and which have been observed by all who have examined the type carefully during the past 15 years (Beidleman, Lowe, Maslin, Wright, Zweifel), match those of the newly acquired six additional specimens of *perplexus*. The type specimen falls at its proper position on the latitudinal clines over the environmental gradient through central New Mexico (tables 1–3; fig. 6). As noted, almost without exception the hybrids (including the type) lie in character-value positions that are intermediate to the means of the frequency distributions of the parental sympatric populations and may lie between the ranges of these distributions as well.

With the type revealed as a hybrid, the *perplexus* problem thus should end after more than a century of perplexing study.

Although the intent of the International Code of Zoological Nomenclature is reasonably clear with regard to hybrids, the Code has remained inadequate for specifically covering the treatment of them (1926, Article 18; 1961, Articles 1 and 17). It has been traditional that names based on specimens that are hybrids become invalid as soon as their hybrid nature is revealed (Mayr, Linsley, and Usinger, 1953, p. 37). However, the matter of the inadequacy of the Code (1961) on this point has been discussed recently by Mayr (1963) and by Smith (1963).

Mayr's (1963, pp. 50–51) straightforward proposal, which meaningfully resolves the matter with a single sentence, is to add the following to the end of Article 24b: "A name given to a species hybrid cannot be applied to either of the parental species." Mayr's stated reasons are biological—they are reasons clearly within the evolutionary framework of biology. For the species hybrids that became inadvertent types, his is the only serious proposal to be made from a genuinely biological point of view and is in keeping with the long tradition and understanding concerning species hybrids. Therefore, it is the one to which we shall continue to subscribe unless and until the International Commission renders a contrary decision. It is painful to feel the need to spell out in words the fact that, in agreeing with Mayr, we assert that a type specimen should actually be of the species that it is designated to represent, rather than an arbitrary specimen as asked for by Smith (1963, p. 50).

Smith (1963, pp. 49–50) wanted to preserve names based on hybrids and invoke the principal of "first reviser" for the allocation of such names. If Smith is concerned primarily with subspecies (gene exchange within the same genetic system) rather than species, as his comments possibly indicated (Smith, 1963, p. 50), we see somewhat less serious consequences (from the biological point of view) in the conservation of names based on such intraspecific hybrids (intergrades). The allocation of these conserved names for subspecies could, as is currently in vogue, be by the first reviser.

However, if a name based on a hybrid were to be conserved and treated strictly *sensu* Smith, by invoking "first reviser," additional problems are immediately encountered, not the least of which is the problem of what constitutes the first revision. If the first reviser for the present species problem in *Cnemidophorus* could be established with wide agreement, which we seriously doubt, that individual would still be a first-reviser-without-knowledge (of hybrid origin) and his "inadvertency" would merely replace the original author's "inadvertency," and biology, at least, would remain to be served (see Mayr, 1963, p. 50).

Of importance in the present situation is the fact that, for many years, the specific name *perplexus* was applied to one of the two parental species (*C. inornatus*) involved in its hybrid origin. And, as might be expected, still more recently the name *perplexus* was applied to the other of its parental species (*C. neomexicanus*), whereas the correct name for the parent *C. inornatus* (*inornatus* versus *octolineatus,* and both of these versus *perplexus*) remains a matter unresolved.[1]

Since 1852 the name *perplexus* has been associated with many species in the genus *Cnemidophorus,* including both of the parental species involved here, and has produced a confusion that is utterly remarkable. The removal of the name from the list of specific names in the genus can only simplify (it cannot complicate) the nomenclature. We can only recommend that the name *Cnemidophorus perplexus* be placed in the Official Index of unavailable names in zoology. Certainly such action cannot be met with

[1] One of the two original cotypes attributed to the collector (William Gambel) of the hybrid type of *C. perplexus* is a specimen of *C. inornatus,* and the other specimen of the pair is the hybrid type—the lectotype by Burt's (1931) revision. It should not go unnoticed, as an example of the "first-reviser" confusion throughout the study of *Cnemidophorus,* that Burt (1931), the major reviser of the twentieth century, not only applied the name *Cnemidophorus perplexus* to *C. inornatus* (as *C. sexlineatus perplexus*) but also lumped virtually all *Cnemidophorus* of the *sexlineatus* group into one species. Moreover, although Burt (1931) is the major reviser of the twentieth century, he is by no means the first reviser.

regret on the part of anyone who has had occasion to work with this group of species.

SYNOPSIS OF TAXA: A synopsis follows for the parental species involved, and for the hybrid that is occasionally formed by their sympatric hybridization. Although a hybrid is often named before its hybrid nature is revealed, such a reptile, that is, a natural hybrid between a uniparental ("all-female") species and a biparental species, has been until now unknown. Natural hybridization between bisexual and parthenogenetic members of the same species was recently reported for *Lacerta saxicola* (Darevsky, 1962; Darevsky and Kulikova, 1961, 1964).

Cnemidophorus inornatus Baird

Cnemidophorus inornatus BAIRD, 1858, p. 255. BURGER, 1950, p. 2. AXTELL, 1961, p. 150.

Cnemidophorus octolineatus BAIRD, 1858, p. 255. AXTELL, 1961, p. 150.

Cnemidophorus sexlineatus perplexus: BURT, 1931, p. 122.

Cnemidophorus perplexus: SMITH, 1946, p. 412. MILSTEAD, 1957, p. 228.

TYPE: U.S.N.M. No. 3032a.

TYPE LOCALITY: Pesqueria Grande (= Villa de Garcia), Nuevo Leon, Mexico.

DISTRIBUTION: Western Nuevo Leon, most of Coahuila, Trans-Pecos Texas, southeastern, southwestern, and northwestern New Mexico, extreme southeastern Arizona, and most of lowland Chihuahua, into Durango. See Wright (1966) for summary of localities of *C. inornatus* in New Mexico.

Localities of known sympatry with *C. neomexicanus* are as follows, all in New Mexico (fig. 1): *Bernalillo County:* 1.6 miles east and 2.7 miles south of Albuquerque. *Dona Ana County:* 8.4 miles west of Hatch. *Hidalgo County:* 14.1 miles northwest (road) of Lordsburg (Pough, 1962). *Otero County:* South Boundary, White Sands National Monument (Lowe and Zweifel, 1952). *Sandoval County:* 1.5 miles north and 16.5 miles west of Bernalillo; valley of the Rio San Pedro, at *ca.* 0.7 mile east of Highway 85. *Socorro County:* McDonald Ranch Headquarters, 4800 feet in elevation, 8.7 miles west and 22.8 miles south of New Bingham Post Office (Lowe and Zweifel, 1952). *Valencia County:* Canyoncito, 5.5 miles east and 2 miles north of Correo.

MATERIAL: The specimens of *C. inornatus* used to obtain the data presented in text are as follows: 8.4 miles west of Hatch, Dona Ana County (M.S.B. Nos. 7864–7892, 7989–7994, 10468–10476); 9 miles east of La Joya, Socorro County (U.A.Z. Nos. 11854–11869; M.S.B. Nos. 8259–8267); San Pedro Creek, 2 miles east and 3 miles north of San Antonio,

Bernalillo County (M.S.B. Nos. 5001–5027); valley of the Rio San Pedro of the Rio Grande del Norte, at *ca.* 0.7 mile east of Highway 85, Sandoval County (U.A.Z. Nos. 11851–11853); valley of the Rio San Pedro of the Rio Grande del Norte (U.S.N.M. No. 30885).

Cnemidophorus neomexicanus Lowe and Zweifel, female × male *Cnemidophorus inornatus* Baird

Cnemidophorus perplexus Baird and Girard, 1852, p. 128; lectotype U.S.N.M. No. 3060 (Burt, 1931), from San Pedro Creek and Tanque Arroyo (valley of the Rio San Pedro of the Rio Grande del Norte), Sandoval County, New Mexico (Wright and Degenhardt, 1962).

Distribution: Known from seven specimens taken in New Mexico at localities of sympatry of the parental species (fig. 1; tables 1–3).

Cnemidophorus neomexicanus Lowe and Zweifel

Cnemidophorus neomexicanus Lowe and Zweifel, 1952, p. 230.
Cnemidophorus perplexus: Maslin, Beidleman, and Lowe, 1958, p. 344.

Type: M.V.Z. No. 55807, collected by C. H. Lowe, field no. 3528.

Type Locality: McDonald Ranch Headquarters, 4800 feet, 8.7 miles west and 22.8 miles south of New Bingham Post Office, Socorro County, New Mexico.

Distribution: Known only from New Mexico, and the vicinity of El Paso, Texas (see Duellman and Zweifel, 1962, fig. 8). Localities of known sympatry with *C. inornatus* are listed above under that species (see fig. 1).

Material: The specimens of *C. neomexicanus* used to obtain the data presented in text, are as follows: 8.4 miles west of Hatch, Dona Ana County (M.S.B. Nos. 7840–7863); 9 miles east of La Joya, Socorro County (U.A.Z. Nos. 11846–11850; M.S.B. Nos. 8268–8270); valley of the Rio San Pedro of the Rio Grande del Norte, at *ca.* 0.7 mile east of Highway 85, Sandoval County (U.A.Z. Nos. 10578, 11870–11878, 11880–11898).

SUMMARY AND CONCLUSIONS

Six specimens of *Cnemidophorus* recently collected in New Mexico are clearly referable to the type of *C. perplexus* Baird and Girard (U.S.N.M. No. 3060, lectotype). These six specimens and the type differ in numerous consistent ways from the sympatric *C. neomexicanus* Lowe and Zweifel and *C. inornatus* Baird. We conclude that all specimens referable to *C. perplexus* are hybrids between *C. neomexicanus* (parthenogenetic) and *C. inornatus* (bisexual) resulting from sympatric hybridization.

Mean hybrid indices (in per cent) for the seven specimens lie on a scale between *C. inornatus* (0%) and *C. neomexicanus* (100%), as follows: scales

around midbody, 29.1; scales between paravertebral light stripes, 0; circumorbital semicircle scales, 37.6; interlabial scales, 77.9; femoral pores, 95.2; toe lamellar scales, 91.9; spotting, 78.3; striping, 55.0; hind-leg pattern, 60.0; ventral body color, 0; tail color, 30.0. The grand mean hybrid index for the characters analyzed is 50.4. Heterosis exhibited by maximum-sized hybrid females, as measured linearly from snout to vent, is on the order of 110–115.

The specific name *C. neomexicanus* is the valid name for lizards referred to *C. perplexus* since 1958. The disposition of the names *C. inornatus* versus *C. perplexus* remains unresolved.

Insofar as we are aware, there has been no other report of a hybrid reptile resulting from a natural (or experimental) cross involving parthenogenetic and bisexual parental species.

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